NOTES AND LITERATURE

MIMICRY IN BUTTERFLIES

American biologists have been somewhat in a quandary of late as to what to believe and to teach about "mimicry" in insects. The consideration of chance resemblances in animate and inanimate things in which mimicry in the strict sense could not possibly exist, and the widespread skepticism of natural selection as an effective, creative agency in evolution have made many of us inclined to bury mimicry in the same grave with telegony, prenatal influences, the inheritance of acquired somatic characters, and sexual selection. Meanwhile, the Oxford school of zoologists, under Professor Poulton's leadership and the inspiration of an orthodox faith in the potency of natural selection, have continued to accumulate a rich array of newly discovered models and mimics among African butterflies.

Many of these and other cases of mimicry are described in the opening chapters of Professor R. C. Punnett's interesting book and admirably portrayed in the sixteen plates, twelve of which are in colors. With a remarkably clear and convincing style that has become familiar to us through his popular little book on Mendelism Punnett here recounts the history of the theories of Bates and Müller, mentions some of the morphological features upon which real affinities among butterflies depend, and describes in some detail examples of mimicry from various parts of the world.

Of particular interest to us in the United States is his brief discussion of the supposed mimicry of *Papilio philenor* by *P. troilus,* by the black southern variety, usually called *glaucus,* of the female of our common *turnus,*[2] and by a third species, *P. asterius* (usually known by us as *P. polyxenes,* or *P. asterias*). The northward extension of the range of *troilus* into Northwest Canada, far beyond that of the supposed model *philenor,* is thought to weaken this as a case of mimicry, and the author concludes that

[1] "Mimicry in Butterflies," by R. C. Punnett, Cambridge Univ. Press, 1915, 8vo., pp. 159, 16 plates.

[2] Punnett transposes these names, following Poulton (*vide Annals Entom. Soc. America,* Vol. 2, 1909, p. 225), who adopts Rothschild and Jordan's revision.

On the whole it seems at present doubtful whether any relation of a mimetic nature exists between *P. philenor* and these three species of *Papilio.*

The blue female of the southern fritillary, *Argynnis diana,* and our "red-spotted purple," *Limenitis* (*Basilarchia*) *astyanax,* which Professor Poulton has conceived also to be mimics of *P. philenor,* are likewise regarded as "very problematically mimetic." The striking resemblance of our "viceroy," *L.* (*B.*) *archippus,* for the "monarch," *Danais* (*Anosia*) *plexippus,* is mentioned, though no allusion is made to Abbott's biometrical study of 87 specimens of the supposed ancestral type, *L.* (*B.*) *arthemis,* from which the mimic, *archippus,* is thought to have arisen. Abbott,* by the way, found that the color markings involved in the Poulton hypothesis of gradual change by natural selection (*e. g.,* reddish spots) are much less variable than the blues and other colors not considered in that theory, the color pattern of *arthemis* showing no tendency to break up or to shift in the direction of the *Anosia* type.

Punnett next examines critically Wallace's well-known laws or conditions of mimicry, discusses the evolution of a Ceylonese "mimicry ring" (a group of five superficially similar butterflies), describes the case of *Papilio polytes,* the trimorphic "mimetic" and "non-mimetic" females of which are genetically separated from one another by two Mendelian factors, considers the enemies of butterflies, and, finally, the relation of seasonal and local variation to mimicry. He arrives at the general conclusion that there are two prominent difficulties in "accepting the mimicry theory as an explanation of the remarkable resemblances which are often found between butterflies belonging to distinct groups," viz., "the difficulty of finding the agent that shall exercise the appropriate powers of discrimination, and the difficulty of fitting in the theoretical process involving the incessant accumulations of minute variations with what is at present known of the facts of heredity."[3] In view of these difficulties, taking his cue from genetics, he suggests that

> Each group of Lepidoptera contains, spread out among its various members, a number of hereditary factors for the determination of color pattern. . . . Some factors may be common to two or more groups, in which case some of the permutations of the factors would be similar in the groups and would result in identical or nearly identical pattern.[4]

* Washington Univ. Studies, Pt. 1, No. 2, 1914.

[3] P. 139.

[4] Pp. 145, 146.

Thus, referring by way of illustration to the somewhat analogous case of the coat colors of rodents, he says:

> In certain features the rabbit might be said to "mimic" the mouse, in other features the guinea-pig.

It is a significant fact in this connection that the various models "mimicked" by the different species of a polymorphic species are almost always closely related, and hence may be expected to exhibit color patterns based on different combinations of identical factors.

In criticism of Wallace's laws of mimicry, Punnett points out the fact that although the mimic and model usually occur in the same locality this is not always the case, the cooperation of migratory birds being invoked to explain the exceptions.

Regarding the defenselessness of mimics as compared with models, it is noted that the "mimic" is often a swifter flyer, and hence better prepared for defense than the model.

Exceptions are given to the rule that the models are more numerous than the mimics, and that the mimics differ from the most of their nearest allies. The Pierid genus *Dismorphia*, for example, includes prominent South American mimics which differ strikingly from the "whites" of the Temperate Zone but, unfortunately for the theory of mimicry, only about a dozen of the seventy-five described species are white, the rest presenting a "wonderful diversity of color and pattern." Among them are species clearly non-mimetic as regards color, which by simple substitution of one color for another in the spots would be transformed into a "mimetic" species.[5]

The author concludes that

> It is on the whole unusual to find cases where a single species departs widely from the pattern scheme of the other members of the genus and at the same time resembles an unrelated species.

Two of the best examples are our American "viceroy" and the pierid *Pareronia*. "Mimicry tends," he adds, "to run in certain groups" and "in many cases at any rate little meaning can be attached to the statement that the imitators differ from the bulk of their allies."

[5] The reviewer recently observed in Porto Rico a case bearing upon this point, in *Leptalis* (*Dismorphia*) *spio*, which closely resembles in color and general shape the very common *Heliconius charitonius*. A color variety of the former, however, is found in certain localities on the island, in which orange replaces yellow in the color pattern, rendering the resemblance to the Heliconian less apparent. A simple mutation of orange into yellow would make this an excellent example of "mimicry."

In the chapter entitled "Mimicry Rings" the author considers the difficulty of explaining the protective value of the minute initial variations in the direction of a model. As an illustration, a group of five superficially similar butterflies in Ceylon is described. This "mimicry ring" includes two hypothetically distasteful Danaines (*D. chrysippus* and *D. plexippus*) and the females of three very unlike males (*Hypolimnas misippus, Elymnias undularis,* and *Argynnis hyperbius*). The coloration of one of these males (*E. undularis*) is a deep purple brown, like that of "satyrs" generally. If this represents the original type from which the gay orange and black pattern of the female has been derived, how has the change come about? Slight initial variations of the Satyr in the direction of the orange Danaine could not possibly be mistaken by birds for the model. The absurdity is pointed out of assuming, on the other hand, that the Danaine was originally like the male Satyr, and acquired its warning coloration *pari passu* with the mimic, for the Danaine model can hardly have been originally like all of the three very diversely colored males of the mimicking females. Mutation in each of the three types, however, may have produced females so similar to the Danaine as to be mistakable for it, and if natural selection indeed operates in this case, it may act in "putting on the finishing touches," or in preventing regression.

In the two following chapters the author discusses the resemblance of two of the three varieties of female *Papilio polytes* to the two "poison-eating" Papilios of India and Ceylon, *P. aristolochiæ* and *P. hector*. As is well-known, Punnett[6] has himself studied in Ceylon the behavior of these species, and Freyer[7] has continued the work, making extensive breeding experiments on the polymorphic "mimic."

A study of the geographical distribution in this case shows a general correspondence between the range of each mimic and its model, but notable differences are discovered.[8] Regarding the value of the resemblance between mimic and model, Punnett had no difficulty in distinguishing between model and mimic on the wing, even at a distance of forty to fifty yards, while near at hand the brilliant scarlet of both models, which covers the body and is conspicuous in spots upon the wings, is seen to be very different from the softer red found upon the wings (not

[6] "Spolia Zeylanica," Vol. 7, Part 25, 1910.

[7] *Phil. Trans. Roy. Soc.*, London, Vol. 204, 1913.

[8] *Vide*: Lutz, AMERICAN NATURALIST, Vol. 45, p. 190, 1911.

upon the bodies) of the mimics. Dried specimens of models and mimics are likely to be confused, but not the living butterflies.

Freyer's breeding experiments bring out the fact that a simple Mendelian relation exists between the three varieties of female in *P. polytes,* the males of which, though phenotypically alike, correspond genotypically to the three kinds of female. Of these three the one resembling the male ("non-mimetic") is recessive to the mimetic forms, lacking a factor, X, possessed either in simplex or duplex condition by the "mimetic" females. The male likewise is latently either xx, XX, or Xx, as the case may be, but retains a uniform appearance in all cases owing to the presence of an inhibitor factor for which he is heterozygous (Ii), the female being recessive (ii). The male, unlike other Lepidoptera, so far as they have been investigated, is also supposd to be heterozygous for a sex factor which we may for brevity call M, responsible for maleness, with which the inhibitor factor is completely coupled, so that the male-producing sperms (MI) always contain the inhibitor factor, the female-producing always lack it (mi).

The two mimetic varieties of female are differentiated from each other by the presence or absence of another factor, Y, which acts merely as a modifier of the factor X when that is present, and transforms the aristolochiæ-like female (XXyy or Xxyy) into the hector-like (XXYY, XXYy, XxYY, or XxYy). This color modifier, responsible for intensifying and extending the red markings, is supposed to occur in either homozygous or heterozygous condition, or to be absent (recessive) in the male-like form of female and also in each biotype of the male, though when present without X, or in the presence of I, it has no visible effect. Thus there are 9 biotypes of males and 3 of male-like females, all phenotypically alike. Referring to Poulton's theory of the gradual evolution by natural selection of the male-like type of female into the aristolochiæ-like, and subsequently into the hector-like, Punnett argues that crossing the hector-like (double dominant) with the male-like (double recessive) germ plasms and inbreeding should show the hypothetical intermediates postulated by Poulton, but no such intermediates have appeared in the breeding experiments.

Freyer's random sampling of the population of *polytes* gave 49 of the two mimetic females to 40 of the male-like coloration, or roughly 5 dominants to 4 recessives, a proportion indicating

stable equilibrium between the mimetic and non-mimetic varieties. Scanty historical data tend to show that the mimics were as common fifty years ago, and probably a century and a half, as to-day, so the author concludes "that in respect of mimetic resemblances natural selection does not exist for *P. polytes* in Ceylon," or at least there is "no effect appreciable to the necessarily rough method of estimation employed."

The author next considers the evidence that the enemies of butterflies could have played the part assigned to them by the advocates of the mimicry theory. Predaceous insects evidently pay no attention to warning colors; certain lizards devour butterflies freely, but do not exercise any discrimination in the species which they attack. Hence neither insects nor lizards can be supposed to play any part in establishing a mimetic resemblance. Birds destroy butterflies in considerable numbers, but

> Some of the most destructive appear to exercise no choice in the species of butterfly attacked. They simply take what comes first and is easiest to catch.

Monkeys and baboons often eat butterflies. They show strong likes or dislikes for certain species. The monkey may be regarded as "the ideal enemy for which advocates of the mimicry theory have been searching—if only it could fly." The conclusion is reached that

> even a slight persecution directed with adequate discrimination will in time bring about a marked result where the mimetic likeness is already in existence. It is not impossible therefore that the establishing of such a likeness may often be due more to the discrimination of the monkey than to the mobility of the bird.

In the final chapter on "Mimicry and Variation" the author describes Carpenter's observations on the polymorphic mimic *Pseudacræa eurytus,* the four forms of which show an extraordinary resemblance to acræine "models" of the genus *Planema.* These butterflies inhabit the shores of Victoria Nyanza in Central Africa where the models are very abundant, the polymorphic mimics less common but still numerous, and intermediates between the different types of mimic rare, but not unknown. On Bugalla Island in the lake, on the contrary, the mimetic Pseudacræas are very abundant, and their respective Planema models relatively rare. Here intermediates between the varieties of the polymorphic mimic occur in proportionately larger numbers than on the mainland, owing as Dr. Carpenter believes to the

cessation of natural selection in the absence of sufficient models to familiarize the hypothetical enemy with the several warning color patterns of the models. On the mainland, however, any of the aberrant intermediates that might be produced by interbreeding of the different varieties of the polymorphic species would meet an enemy having constant experience with the warning colors of the different models, and tend to be eliminated. The enemy, in other words, would avoid the perfect mimics, while aberrant individuals suggesting two models at once presumably would be attacked and eaten. This interesting case deserves thorough investigation.

The author makes a *faux pas* when he says regarding seasonal variations in butterflies, due to "changes in the conditions of later larval and earlier pupal life":

> In no case are they known to be inherited, and in no case consequently could variation of this nature play any part in evolutionary change.

In the example cited (*Araschnia levana-prorsa*), which presents two color patterns alternately through the year, it is obvious that both patterns are inherited. The environment indeed decides which shall appear, but the hereditary basis common to both seasonal types is no less real than that of any butterfly of seasonally uniform pattern. Although the seasonal color patterns of *A. levana* and *prorsa* apparently can not behave as Mendelian allelomorphs to one another as do the color patterns of other non-seasonal polymorphic insects, they are by no means outside the pale of Mendelian heredity. It is not too much to expect that future studies will disclose colors or color patterns allelomorphic to *A. levana-prorsa's* shifting coloration. The reviewer would not, with Professor Punnett, rule seasonal variation entirely out of court as possible stages in "the development of a mimetic likeness" or, rather, in the evolution of the remarkable likenesses, alleged to be mimetic, which this book brings so well to our attention.

The author is so strongly influenced by the idea that minute variations are fluctuations always controlled by the environment rather than by the internal conditions that result in heredity that he treads upon uncertain ground in discussing an example of local variation cited by Poulton.[9] A small white spot on the wing of *Danais chrysippus* varies in size locally from a conspicuous marking, in China, to a faint dot tending to dis-

[9] Bedrock, 1913, p. 300. Cited by Punnett.

appear, in Africa. Punnett suggests that the details in pattern may be in slight measure affected by the plant species on which the caterpillars have fed, thereby producing local races. Transportation of a local race to a region inhabited by another distinct local race "would help us in deciding whether any variation by which it is characterized had a definite hereditary basis or was merely a fluctuation dependent upon something in the conditions under which it had grown up." We may well ask: are these two propositions mutually exclusive? May not a detail of color pattern to a certain degree at certain times be subject to environmental influences and at the same time may not its variations have a "definite hereditary basis?" The reviewer has had so much experience in observing the transmission in *Colias philodice* and *C. eurytheme* of spots comparable to that mentioned in *D. chrysippus* that he is convinced that a definite hereditary basis (consisting presumably of multiple factors) underlies every fluctuating detail of color pattern. By artificial selection from inbred stock, using uniform food plants, and exposing the caterpillars and pupæ to similar conditions, the breeder of butterflies may decrease even to elimination or increase within certain limits a detail of color pattern like that mentioned. The champions of the theory of mimicry are entitled to this crumb of comfort. "For if it can be supposed," remarks the author, "that small differences of this nature are always transmitted, it becomes less difficult to imagine that a mimetic resemblance has been brought about by a long series of very small steps."

Yet the facts which the mimicry theory seeks to explain clamor for explanation. Punnett sets forth at the end some that are most insistent.

> Certain color schemes are characteristic of distinct geographical regions in South America, where they may occur in species belonging to very different genera and families.

In Central America a pattern occurs that is common to several Heliconines, Ithomiines, Nymphalines of two or more genera, and Pierids; in eastern Brazil another pattern in which "all the various genera which figure in the last group are again represented." On the upper Amazon a still different pattern is common to the same group of genera from that just mentioned, only two notable genera being absent. Finally in Ecuador, Peru and Bolivia a widely different pattern occurs in a group lacking

a Pierid or Danaid but containing in exchange "a *Papilio*, an *Acræa*, and two species of the Satyrid genus *Pedalodes*."

Assuming that one of these patterns must have been the most primitive, he asks why a distasteful genus should change from one efficient warning pattern to another quite distinct one. Though the premise is not necessarily true nor even probable, yet if the ancestral pattern were a generalized type of any "warning" character whatever, the question would still be pertinent.

The author suggests that a newly acquired color scheme, like one of these, may be "associated with a certain physiological constitution which places butterflies possessing it at an advantage as compared with the rest," just as the melanic variety of peppered moth that is ousting the typical form in Britain and on the Continent may have associated with its deep pigmentation a greater hardiness. This, however, goes but a short way toward the explanation of the extraordinary local associations of unlike South American butterflies showing similar coloration. This is a live question that challenges the attention of any student of evolution who has opportunity to undertake experimental work in the tropics of South America.

So if we must sooner or later consign Mimicry to its last resting place, with its less infirm but already moribund parent, Warning Coloration, let us do so filled with gratitude for the pioneer work accomplished by its champions in opening up promising fields of investigation, where we or our descendants may hope to discover new factors in evolution or to gain a deeper insight into those now only dimly understood. Thanks are meanwhile due to the author of this attractive volume for his keen diagnosis of the present condition of the mimicry theory and for his admirable description of the phenomena which it has attempted to explain.

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